Shifting baselines in a changing world: Identifying management targets in endangered heathlands of the Cape Floristic Region, South Africa

Cherié J. Forbes*,[1], Lindsey Gillson, M. Timm Hoffman

Plant Conservation Unit, Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch, 7701, South Africa

A B S T R A C T

Ecological baselines are important in informing conservation management targets. Baselines can shift, however, depending on the timescale of observation. Using observations from the past few years or decades can give a misleading impression of the normal range of variability of an ecosystem, and the extent of recent human transformation. Palaeoecological techniques can track interacting effects of climate change and land-use on vegetation composition and fire regimes over decadal–millennial timescales, thereby informing ecologically possible management options.

In the Cape Floristic Region, South Africa, European settlement and subsequent land transformation led to dramatic changes in land-cover. Ninety-six percent of Renosterveld, a highly diverse indigenous shrubland, has been transformed. Thus, appropriate management of remaining Renosterveld fragments is critical to biodiversity conservation in this endangered habitat. However, we know little of the Renosterveld landscapes before colonial settlement from the mid-17th century.

This study used fossil pollen, coprophilous fungal spores and charcoal to track vegetation, herbivory and fire at centennial timescales in one of the few remaining Renosterveld fragments. Results showed that the current landscape at the study site is atypical compared with the long-term history of the site, with higher abundance of Renosterbos (*Elytropappus rhinocerotis*) and local fires and herbivory that reflect intensive utilisation beginning in the mid-20th century. Managing the integrity and composition of Renosterveld at this site according to a pre-colonial baseline will require lower levels of herbivory and less frequent fire.

This study illustrates how palaeoecological techniques can inform conservation management and restoration targets. To accommodate uncertainties in future environmental change, we recommend an adaptive management approach, which incorporates palaeoecological analyses, burning and grazing experiments and long-term monitoring.

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1. Introduction

Many human-impacted landscapes require pro-active conservation management efforts in order to maintain biodiversity, and to restore heterogeneity and resilience. Choosing land-use management targets is complex, however, especially when long-term data are lacking. Pauly (1995) described the 'shifting baselines syndrome', whereby each new generation of observers defines their frame of reference based on observations made within their lifetime. The danger of this approach is that the past few decades may not be representative of the normal range of variability of an ecosystem or population. Longer-term data are therefore needed to set ecologically realistic management targets. Most neoecological studies are characterized by relatively short-term perspectives, which consider annual to decadal timescales of usually less than 60 years. Past studies show that short-term perspectives, often based on collective societal memory and reflections, often provide an unrealistic interpretation of environmental baselines and change (Gillson, 2015; Wolfe et al., 2012). Palaeoecological data can be used to develop a longer-term perspective, however, that considers centennial to millennial timescales.

A palaeoecological perspective on environmental change provides improved evidence of historical variability and an opportunity to identify drivers of environmental change. Palaeoecological data are a valuable but often under-utilised temporal source, since the recorded timescales precede monitored or surveyed data. Vast potential exists to use such long-term information to set more ecologically realistic management and restoration goals. While this approach has successfully guided management of some freshwater ecosystems (Battarbee and Bennion, 2011; Bennion et al., 2011; Gell et al., 2013; McLoughlin et al., 2011; Wolfe et al., 2012), forest ecosystems (Cyr et al., 2009; Long, 2009), and in fire management (Huerta et al., 2009; Whitlock et al., 2010), its use is still relatively scarce, leaving opportunities for wider application (Gillson, 2015; Gillson and Marchant, 2014).

This study applies a palaeoecological approach to identify a vegetation state that reflects a pre-colonial baseline in an endangered heathland in the Cape Floristic Region (CFR) of South Africa, one of 25 global biodiversity hotspots (Mittermeier et al., 1998). The CFR is both the smallest and richest internationally recognized floral kingdom containing >9000 plant species, of which 68% are endemic (Goldblatt and Manning, 2000; Manning and Goldblatt, 2012; Myers et al., 2000). It is a global conservation priority because of its species richness, endemism and rates of transformation; about 30% of the CFR's primary vegetation has already been lost. Renosterveld is the most highly threatened vegetation type in the CFR. Only 4% of Renosterveld's original cover remains with remaining fragments critically endangered and under significant pressure as a result of habitat transformation attributable to agriculture (including crop cultivation (Fig. S1 in Supplementary data) and inappropriate grazing and fire regimes), urban development, unsustainable harvesting, and the spread of invasive alien species (Rebelo et al., 2011; Rouget et al., 2003a,2003b; von Hase et al., 2003). Climate change provides a further threat to its unique biodiversity (Cowling et al., 1997; Fairbanks et al., 2000).

The high level of transformation further suggests that biodiversity and ecosystem services, such as water purification, nutrient cycling, pollination, resistance to alien plant invasion, and erosion regulation, are at risk. Furthermore, remaining fragments are under pressure from grazing by livestock and reintroduced large indigenous herbivores (Cowling et al., 1986; Low and Jones, 1995). While the conservation and restoration of scarce remaining fragments of Renosterveld is urgent, limited information exists on which to base management targets, because few ecological studies were completed before intensive land-use and habitat transformation began (Kraaij and van Wilgen, 2014). For example, little is known about the origin and composition of Renosterveld and whether current burning and grazing regimes are comparable to pre-colonial baselines. There are conflicting descriptions of 'pristine' Renosterveld, especially with regards to the relative abundance of grasses and shrubs, depending on the temporal frame of reference (Cowling et al., 1986; Curtis, 2013; Curtis and Bond, 2013). The uncertainty of the composition of Renosterveld makes it difficult for conservationists and environmental managers to build evidence-based and contextual arguments for conservation, restoration and ecosystem services management. Therefore, the land-use impact by various human groups requires investigation: what was the impact of European settlers on Renosterveld composition? Is the current relative abundance of grasses and a common asteraceous shrub called Renosterbos (*Elytropappus rhinocerotis*) typical? Furthermore, what does the palaeoecological record reveal about the impact by European settlers and the subsequent period of agricultural intensification on Renosterveld species composition? Can a long-term, palaeoecological-perspective provide insight into whether the long-term variability has been exceeded, potentially compromising ecological resilience?

Comparing the Renosterveld composition under the influence of climate variability and land-use by European farmers and conservation requires high resolution, multi-proxy palaeoecological studies, coupled with known historical and neoecological studies. Therefore, we conducted a palaeoecological investigation of the Elandsberg Private Nature Reserve (thereafter, Elandsberg PNR), one of the few remaining Renosterveld ecosystems, with the aim of informing land-use management recommendations. Using regional palaeoclimate data as a guide, we considered the effects of a known warm event, the Medieval Climate Anomaly (MCA) and a known cold event, the Little Ice Age (LIA). We reconstructed vegetation composition, levels of herbivory and fire history using fossil pollen, coprophilous fungal spores and charcoal. We then interpreted the findings in terms of ecological resilience. We also used the data as a basis for recommending changes in the management of fire and herbivory, as well as informing the design of grazing and fire management experiments at the site.

2. Renosterveld environments

2.1. Vegetation, soils and climate

Renosterveld is an evergreen, fire-prone Mediterranean-type shrubland or asteraceous shrubland with mainly tussock (bunch) grasses and a high diversity of geophytes (Rebelo et al., 2006; Specht and Moll, 1983). Renosterveld typically occurs on fine-grained, nutrient rich substrates at the ecotone between Fynbos and Succulent Karoo biomes. This study focused on the West Coast Renosterveld vegetation type, which is located in the winter rainfall zone (WRZ) of the CFR. It therefore experiences a Mediterranean-type climate characterised by summer drought and maximum rainfall during the winter season (Chase and Meadows, 2007; Haensler et al., 2011; Midgley et al., 2003). In the past 2000 years, the region has experienced periods of significant climatic variability, including the globally recognised MCA (ca. CE 900–1400) and LIA (ca.CE1400–1800) (Nicholson et al., 2013). Previous palaeoclimatic studies in the southern African region indicate that the MCA was warm and arid compared to the subsequent colder, wetter LIA (Holmgren et al., 2003; Huang et al., 2000; Lee-Thorp et al., 2001; Stager et al., 2012; Tyson and Lindesay, 1992). Instrumental records show that further climate change, characterised by a warming trend, occurred in the latter part of the 20th century (Cronin et al., 2003; Haensler et al., 2010). Climatic projections for the region suggest increasing aridity in the coming decades, associated with higher temperatures and a shorter rainy season, threatening both agriculture and biodiversity conservation. Researchers have predicted range contractions, localised shifts and/or species turnover in both Fynbos and Succulent Karoo vegetation for the next 50 years as a result of climate and land-use change (Haensler et al., 2011; Midgley and Thuiller, 2007; Niekerk et al., 2012; Toggweiler and Russell, 2008).

2.2. Land-use history and pre-colonial renosterveld composition

The CFR has a long history of land-use. San hunter-gatherers were in the region from at least 25,000 BP to the historical period while Khoikhoi pastoralists introduced livestock to the Western Cape approximately 2000 BP (Deacon, 1992; Boonzaier, 1996). San hunter-gatherers are thought to have had minimal impact on the land (Deacon, 1992), whereas Khoikhoi pastoralists used intense 1–4 year fire cycles as a mechanism to improve pastures for grazing (Botha, 1924; Neumann et al., 2011; Smith, 1987). Thereafter, the arrival and colonisation of European settlers since the mid-17th century resulted in increased grazing pressure as well as the introduction of crop cultivation. European settlers also used a combination of fire suppression in some areas to protect agriculture and property, and

regular burning in others (Bergh and Visagie, 1985; Hoffman, 1997; Newton, 2008). In the 20th century, agricultural intensification increased the impact on the environment.

2.3. Elandsberg Private Nature Reserve

Elandsberg PNR is a Stewardship Contract Nature Reserve about 3500 ha in extent, situated on Farm Bartholomeus Klip (33.45000 S and 19.05000 E). It is important for conservation since it contains one of the largest areas (ca. > 1000 ha) of remaining West Coast Renosterveld and is habitat for the endemic, critically endangered geometric tortoise (*Psammobates geometricus*), one of the rarest tortoises globally (Low and Rebelo, 1996) (Fig. 1). The geology is predominantly composed of terrace gravel and alluvial debris, with patchy areas of Malmesbury shales in the centre (Mucina and Rutherford, 2006; Newton and Knight, 2005). The reserve is generally stony and therefore not suitable for extensive cultivation, though some areas (i.e. old lands; Fig. 1) supported the limited cultivation of wheat and other grain crops before proclamation of the conservation area in CE 1973. The most important land-use before CE 1973 was grazing by cattle and sheep. Although the reserve after CE 1973 functioned primarily for the conservation of the geometric tortoise, large indigenous herbivores were also reintroduced to the reserve (i.e. eland (*Taurotragus oryx*), blue wildebeest (*Connochaetes taurinus*), black wildebeest (*Connochaetes gnou*), zebra (*Equus* spp), red hartebeest (*Alcelaphus buselaphus*), gemsbok (*Oryx gazelle*), bontebok (*Damaliscus dorcas dorcas*) and springbok springbok (*Antidorcas marsupialis*)) (Wooding, 2011). The area to the west of the Elandsberg PNR is transformed, highly fragmented, privately-owned land that is mostly used for agriculture.

3. Methodology

Using an aluminium pipe of 8 cm diameter, we extracted a sediment core (henceforth, VANG core) from a wetland basin of ±22.5 m diameter, called Vangkraal Spring, located at 33.4383167 S and 19.068967 E and 151 m above sea level. We conducted a survey of the vegetation surrounding the Vangkraal Spring wetland by examining patches of different vegetation and assessing vegetation biodiversity within eight plots, 5×10 m in size. We identified and named the eight vegetation units: Shale Renosterveld, Alluvium Fynbos, Renosterveld-Fynbos Ecotone, Grassland, Grassland-Renosterveld matrix, Olive stand, Thicket and a Wetland vegetation unit that incorporated the vegetation immediately surrounding the Vangkraal Spring itself (Fig. 2a; Supplementary data Fig. S2 and Table S1). We recorded the dominant species and their respective percentage abundance in each plot, and classified less abundant species with less than 1% cover as 'other'. We compared the presence and relative abundance of the dominant species, families and genera in the vegetation survey with the pollen types/taxa found in the surface sediment sample to evaluate the relationship between the modern vegetation type (as determined by the vegetation survey) and the pollen spectra (as per the modern pollen 'rain' determined by the surface sample).

3.1. Fossil pollen, spore and charcoal analysis

The VANG core was 87 cm long but only 54 cm was used for pollen analysis because of poor pollen preservation in the deeper sediment layers. The VANG core was also used for the analysis of coprophilous fungal spores and charcoal (macro- and micro-charcoal) abundance, organic carbon abundance (Loss on Ignition)
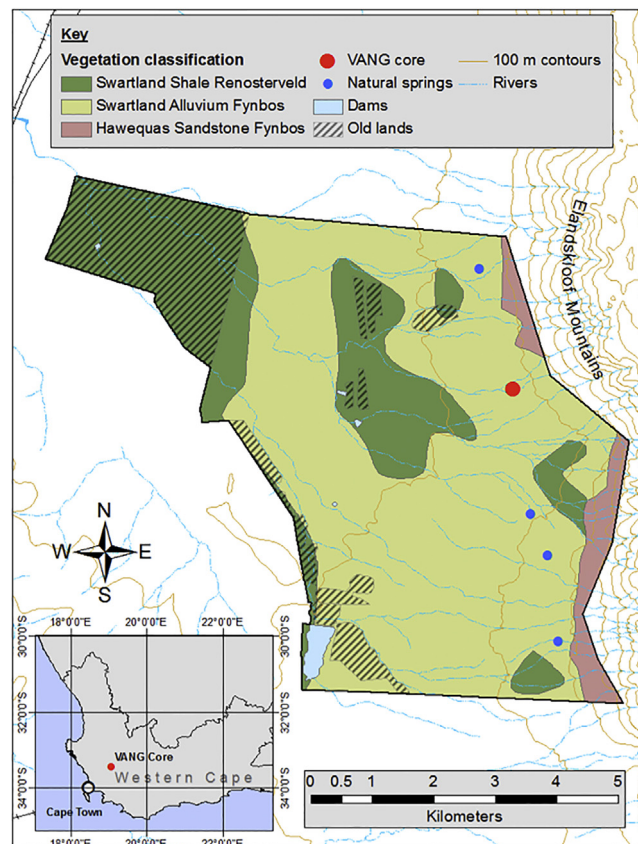

Fig. 1. Map of Elandsberg PNR study site (33.45000 S and 19.05000 E) showing location of Vangkraal Spring wetland where the 'VANG' sediment core was retrieved (red dot; 33.4383167 S and 19.068967 E). Blue dots represent other springs occurring in Elandsberg PNR. Diagonally crossed areas represent old lands that were previously cultivated. The red box represents the approximate study area shown in Fig. 2a.
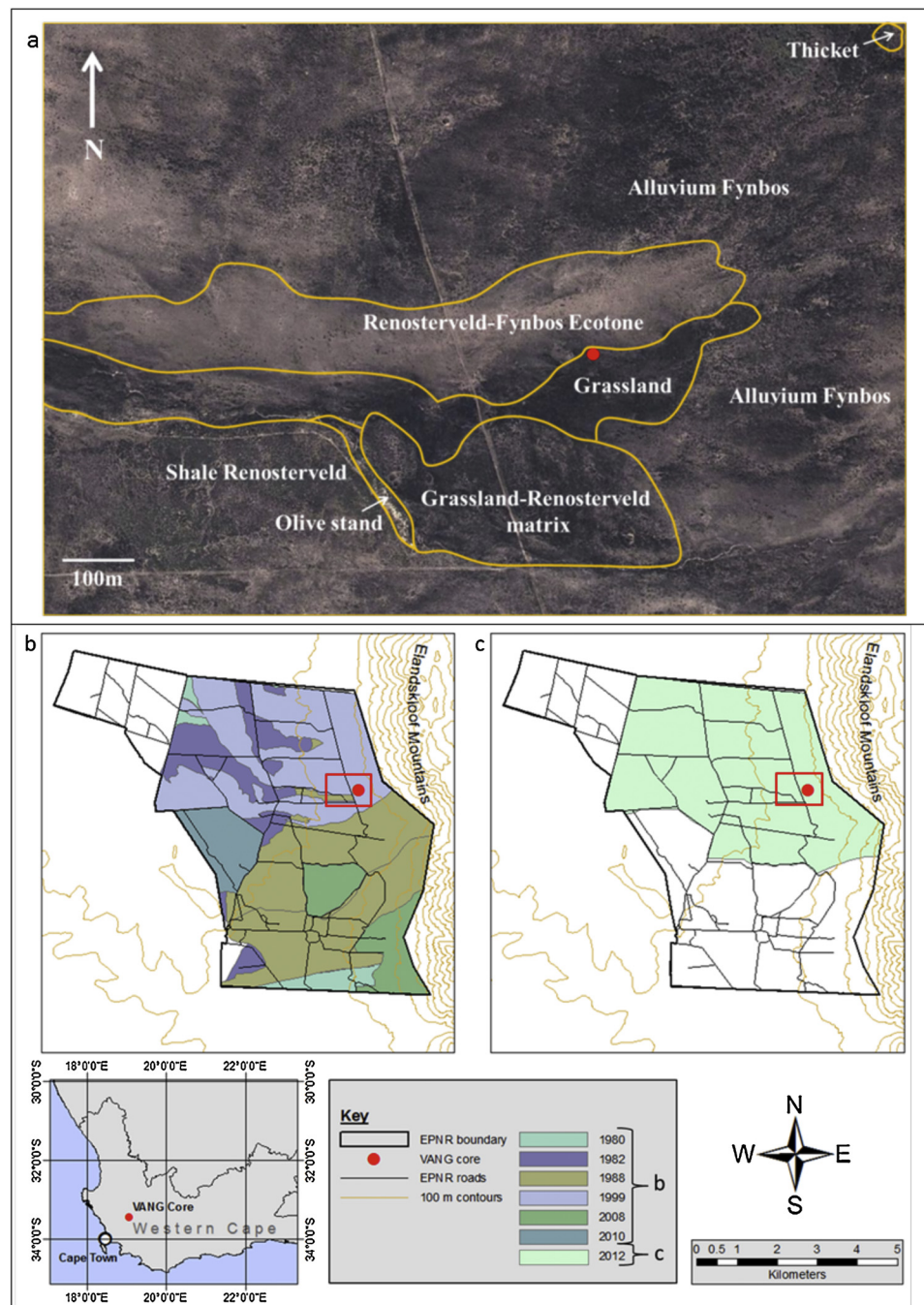
Fig. 2. (a) Map of the study area at Elandsberg PNR in 2013. Demarcated areas (in yellow) represent vegetation units that were chosen according to the most dominant vegetation type present in the vegetation survey. Map of Elandsberg PNR showing fire history from (b) 1980–2010 and (c) the most recent fire in 2012. Roads are included since they often act as fire breaks. The 'VANG' sediment core was retrieved from Vangkraal Spring wetland which is marked by the red dot; 33.4383167 S and 19.068967 E. The red box in Fig. 2(b) and (c) represents the approximate study area shown in Fig. 2a.

and inorganic carbonate content. Sediment was described using a modified Troels-Smith protocol (Troels-Smith, 1955). Sub-samples of 1 cm^3 of sediment were prepared for pollen, spore and charcoal analysis using standard procedures outlined in Bennett and Willis (2001) which removed sulphur compounds, carbonates, humic acids, macrofossils, silicates and cellulose. An exotic spore (*Lycopodium*) was added for pollen, charcoal and spore concentration calculations (Bennett and Willis, 2001). A minimum pollen sum of 250 and maximum of 327 terrestrial pollen grains (excluding aquatics and marginal pollen types, Cyperaceae and *Polygonum*) were counted to allow for statistical significance

(Barkley, 2009; Hill, 1996; Keen et al., 2014; Maher, 1972; Quick et al., 2011; Trombold and Israde-Alcantara, 2005). We excluded aquatic and marginal pollen types from the pollen sum because the focus of this study was the wider terrestrial landscape, rather than the wetland vegetation. The abundance of aquatic and marginal pollen types (Cyperaceae and *Polygonum*) were calculated relative to total pollen count (i.e. total aquatic and marginal pollen /(terrestrial pollen) and were presented as 'aquatics and marginal: terrestrial pollen' in the pollen diagram. Pollen was identified using a reference slide collection, general pollen reference books (Bonnefille and Riollet, 1980; Moore et al., 1991) and the African

Pollen Database (http://medias3.mediasfrance.org/pollen/). We classified unidentifiable pollen as either 'unknown', 'concealed' or 'degraded'. These concealed and degraded grains were not included in the pollen sum. A range of coprophilous fungal spore types (including *Sporormiella*, Sordariaceae, *Gelasinospora* and *Coniochaeta*) were used to track herbivory over time, rather than relying solely on the widely accepted coprophilous fungal spore type, *Sporormiella* (Baker et al., 2013; Carrión et al., 2000; Gelorini et al., 2011; Graf and Chmura, 2006; van Geel and Aptroot, 2006). A minimum of 100 coprophilous fungal spores and 100 *Lycopodium* exotic spores were counted for each sub-sample. However, when coprophilous fungal spores were scarce, counting of coprophilous fungal spores continued until 100 terrestrial pollen grains were encountered, to ensure statistical robustness (Gelorini et al., 2012). We calculated pollen and spore concentrations by using the following equation modified from Bennett and Willis (2001):

$$Fossil\ pollen\ or\ spore\ concentration = (Lycopodium\ added$$

$$x\ fossil\ pollen\ or\ spore\ counted)/(Lycopodium\ counted)$$

Micro-charcoal ($<150\ \mu m$) abundance was determined using point count estimation (Clark, 1982). Micro-charcoal particles greater than $10\ \mu m$ were recorded at $400\times$ total magnification. A minimum of 200 items (i.e. the sum of charcoal hits and *Lycopodium* spores), with at least 100 charcoal particles, were counted in each sample (Duffin et al., 2008; Finsinger and Tinner, 2005). Macro-charcoal particles ($>150\ \mu m$) were recovered during the sieving of the pollen preparation and were counted at 10x magnification. Macro- and micro-charcoal particle abundance was measured for each of the 36 depths where pollen and spore abundance was measured. However, we analysed an additional 11 samples in the lower depths (i.e. 35–53 cm) of the VANG core for micro-charcoal abundance to determine the patterns that emerged. As a result, of the 54 cm VANG core, every 1–2 cm (a relatively high resolution by most palaeoecological standards) was counted for pollen, spores and charcoal to explore the relationship between vegetation, herbivory and fire.

Pollen data is represented as a percentage of total pollen sum. Although this method of representation of pollen percentage data is common in palaeoecology (Meadows et al., 2010; Meadows and Baxter, 1999; Neumann et al., 2011; Quick et al., 2011; Sugita, 1994; Webb et al., 1981), percentage data may show evidence of the 'Fagerlind effect', whereby changes in the abundance of one taxon will affect all of the others (Fagerlind, 1952; Prentice, 1988). For this reason, during the interpretation of the palaeoecological data, concentration data (see Supplementary data – Fig. S3) was used alongside the percentage data (see Fig. 4a and b) in order to identify any spurious trends caused by the Fagerlind effect and allow a more nuanced interpretation of trends observed. Zonation of pollen data was carried out using cluster analysis based on 70% minimum resemblance levels in PRIMER (Version 6.1.5, Primer-E Ltd, Plymouth, United Kingdom). Untransformed pollen, spore and charcoal data were plotted in pollen diagrams generated using C2 Version 1.5 (https://www.staff.ncl.ac.uk/stephen.juggins/software/C2Home.htm).

3.2. Accelerator mass spectrometry (AMS) radiocarbon dating and Lead-210 (^{210}Pb) dating

We used three AMS radiocarbon dates (for depths 31.5 cm, 46 cm and 54 cm) and ^{210}Pb dating (seven samples ranging from depths 0–25 cm) to establish a chronology for the VANG core. Sediment samples for AMS radiocarbon dating were analysed by Beta Analytic Inc. Laboratory in Florida at the North American Facility Headquarters. The samples dated were the bulk organic fraction that remained after sieving the sediment to $<150\ \mu m$ to remove any roots or macro-fossils.

Thereafter, an acid-alkali-acid (AAA) pre-treatment was applied to remove possible contamination from bicarbonate in the water, humic acids from decaying plants, dissolved carbon dioxide from the atmosphere, and carbon from humus leaching or adsorbing down the sediment profile. The AMS radiocarbon dates were calibrated online using a Bayesian radiocarbon calibration tool, BCal (http://bcal.shef.ac.uk/) (Buck et al., 1999) and the southern hemisphere calibration curve. Core Scientific International in Canada analysed sediment samples for ^{210}Pb. The ^{210}Pb and AMS radiocarbon dating results were combined in an age-depth model using a 'cubic spline' interpolation (Colman et al., 2009; Huerta et al., 2009; Walsh et al., 2010) using the Clam package version 2.2 (Blaauw, 2010) in R (http://www.R-project.org/). We plotted modelled calibrated ages, generated using Clam, next to the pollen, spore and charcoal data using C2.

4. Results

4.1. Vegetation survey of Elandsberg PNR study area

Fig. 2a, Fig. S2, and Table S1 of the Supplementary data show and describe different vegetation units in the vicinity of Vangkraal Spring wetland. The most dominant species in each vegetation unit are: *Protea* spp in Alluvium Fynbos, *Themeda triandra* in the Renosterveld-Fynbos Ecotone and Grassland, *E. rhinocerotis* in Shale Renosterveld and Grassland-Renosterveld matrix, *Olea europea africana* in Olive stand, *Olea europea africana* and two *Searsia* spp in Thicket, and Cyperaceae in Vangkraal Spring Wetland.

4.2. Sediment description

The deepest section of sediment where fossil pollen was recovered (41–54 cm) consisted of a majority of coarse sand with some fine sand and silt (Gs2, Ga1and As1). Here no vegetative matter was found Fig. 4b). The majority of the sediment which made up the VANG core (12–41 cm) consisted of a black brown matrix of fine sand, silt and clay with occasional small rootlets and stems from herbaceous plants (Ga3, Ag/As1 and Th^{+1}) (Fig. 4b). The top 12 cm of the core was very black in colour, consisted of mostly fine sand and clay and of highly humified organic matter and a considerably densely packed amount of rootlets and stems of herbaceous plants (Ga2, As1 and Th1) (Fig. 4b).

4.3. Chronology

AMS radiocarbon dating showed a basal age of ca. CE 750 at a depth of 54 cm. Table 1 shows additional dates. Measurable quantities of ^{210}Pb were found in the VANG core between 0–25 cm, suggesting an age of ca. CE 1915 at 25 cm (Fig. 3). The radiocarbonand ^{210}Pb dates suggest slow sediment accumulation (0.17 mm per year) between 54 cm and 46 cm, followed by higher sediment accumulation (0.63 mm per year) from 46 to 31.5 cm. Compared to most depths (below 25 cm) of the VANG core, samples that were ^{210}Pb dated had a generally higher or faster sediment accumulation rate (mean 0.788 g/cm^2/yr). Furthermore, the dates for the introduction of exotic taxa such as various cereal crops (Cerealia) and alien trees (*Eucalyptus* and *Pinus*) in South Africa and land-use data specific to the Elandsberg PNR (Becker, 1996) were also used for calibration and provided relative age horizons (see Table S2 for specific dates, sources and references for the introduction of alien plants).

4.4. Fossil pollen, spore and charcoal analysis

Fig. 4a presents selected pollen, spore and charcoal trends. Fig. S3 of the Supplementary data provide data for pollen

Table 1
Results obtained from (a) ^{210}Pb dating for seven samples from depths 0 to 25 cm and (b) AMS radiocarbon dating for three samples from 31.5 to 54 cm for the VANG core.

a)

Sample name/ laboratory code	Sample depth (cm)	Age at Bottom of Extrapolated Section in yr BP (constant rate of supply CRS model estimate)	CRS Sediment Accumulation Rate (g/cm²/yr)	[210]Pb Total Activity (DPM/g)	[210]Pb Unsupported Activity (DPM/g)	Error [210]Pb +/- 1 S. D. (DPM/g)	Calendar years (AD)
VANG01 (07122013-1)	0–2	3.239	0.934	13.222	11.482	0.45	2008
VANG02 (07122013-2)	2–5	9.520	0.881	12.584	10.844	0.44	2002
VANG03 (07122013-3)	5–8	16.296	0.851	11.089	9.349	0.42	1996
VANG04 (07122013-4)	8–11	24.420	0.809	10.014	8.274	0.40	1988
VANG05 (07122013-5)	11–15	35.260	0.791	7.709	5.969	0.35	1977
VANG06 (07122013-6)	15–20	53.695	0.719	6.684	4.944	0.32	1958
VANG07 (07122013-7)	20–25	97.070	0.530	5.682	3.942	0.30	1915

b)

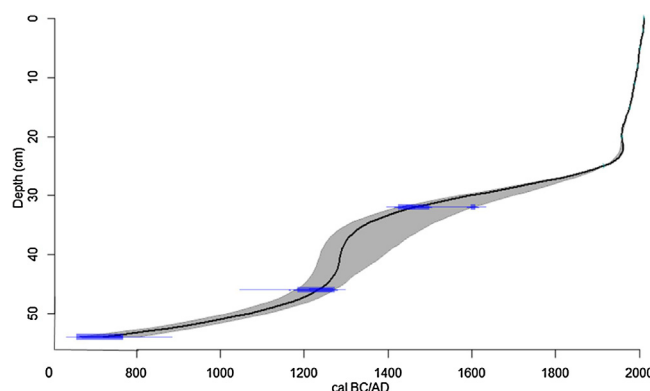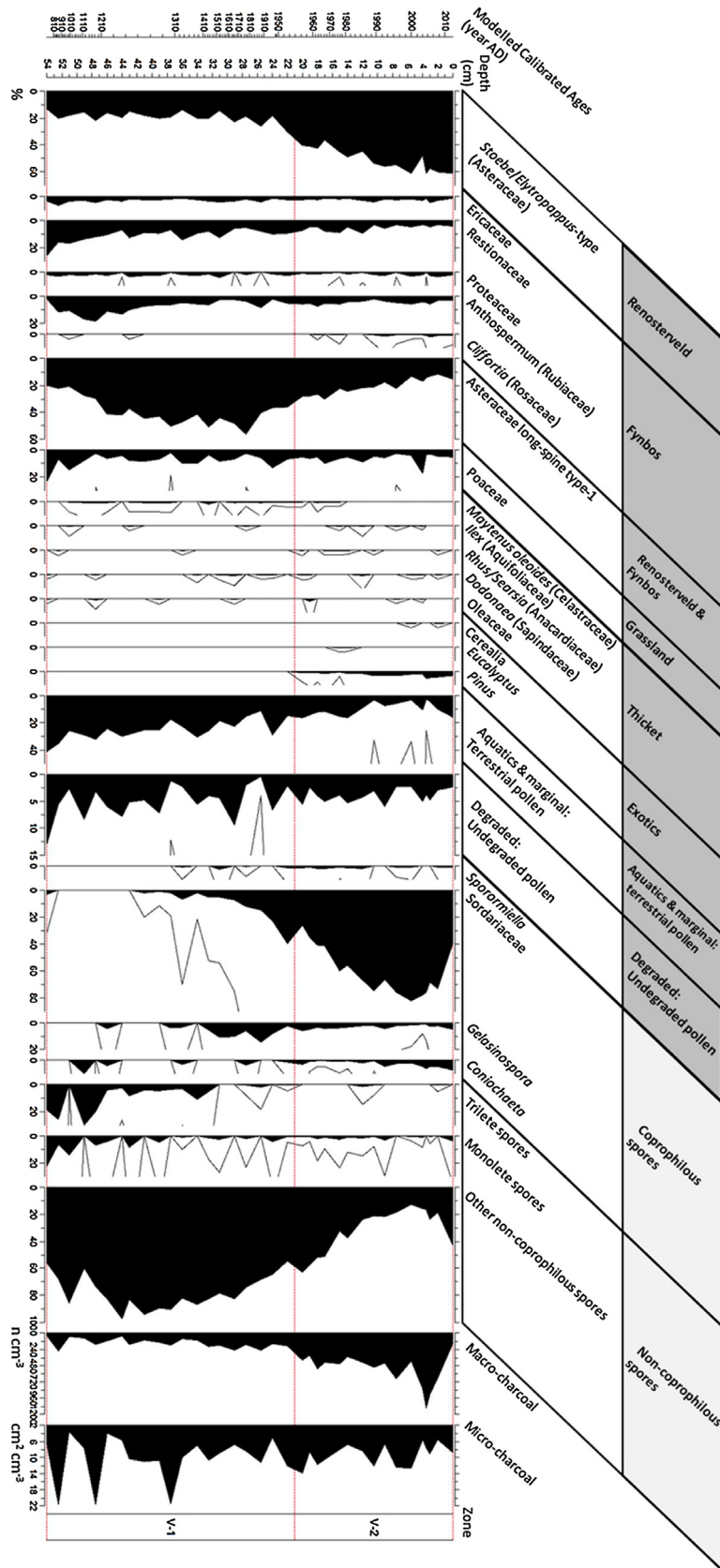| Sample name/laboratory code	Sample depth (cm)	Radiocarbon date (yr BP)	BCal Calibrated date (cal yr BP)	Probability (Standard deviation and %)	Calendar years (AD)
VANG31.5cmCJF2 (364264)	31.5	470 ± 30	524–451 and 355–388	2 SD (95%)	1452
VANG46cmCJF3 (364265)	46	850 ± 30	769–677	2 SD (95%)	1223
VANG54cmCJF1 (336277)	54	1350 ± 30	1199	2 SD (95%)	751

Fig. 3. Age-depth model for samples from 0 to 54 cm for the VANG core including the following: the date that the core was extracted (AD 2012), seven ^{210}Pb dates and three radiocarbon dates with ±SD error bars.

concentration. Differences between the percentage and concentration diagrams are due to the Fagerlind effect (seen in the percentage diagram – Fig. 4a). Using percentage and concentration data together facilitates comparisons and the identification of patterns that are robust across both data types. In this instance, concentration and percentage data showed similar trends, except for changes in Asteraceae long-spine type-1 and 'Other non-coprophilous spores', which only showed in the percentage data and were therefore attributed to the Fagerlind effect. As a result of the 70% minimum resemblance levels of the cluster analysis performed in PRIMER, the presence of two statistically significant zones was revealed, V-1 (21–54 cm) and V-2 (0–21 cm), which explained 21.3% of the variance in the data. The number and position of the zones were the same in the percentage (Fig. 4a) and concentration data (Fig. S3). Terrestrial pollen taxa with abundance > 2% were grouped into species characteristic of the various vegetation units (see Section 4.1.

above and Table S1 of the Supplementary data for descriptions of the vegetation units).

4.4.1. Zone V-1 (20 sub-sample depths; 21–54 cm)

Zone V-1 comprised 20 sub-samples, dating from ca. CE 750–1955 (54 cm–21 cm) and was characterised by a high abundance of Asteraceae long-spine type-1 pollen (average of 31%). Asteraceae *Stoebe/Elytropappus*-type pollen was the next most abundant pollen type in this zone, with an average of 19% and reached its lowest (13%) in ca. CE 750 (54 cm). The following taxa reached their highest abundance during this zone: *Anthospermum (Rubiaceae) (18%), Ericaceae (7%), Proteaceae (4%), Restionaceae (26%) and Poaceae (23%)*. Total aquatics and marginal pollen types (Cyperaceae and *Polygonum*) were higher in Zone V-1 than Zone V-2 with a mean of 25%. The ratio of degraded pollen to undegraded (terrestrial pollen) was only slightly higher in this zone (mean ratio of 0.05) than in the rest of the sequence.

Fig. 4. (a) Percentage diagram for selected pollen taxa from the VANG core. The pollen sum included terrestrial and unknown pollen. x10 exaggeration is shown since percentage values are often low for most taxa. (b) Summary pollen percentage diagram with all taxa grouped into major vegetation types. Zonation is calculated by cluster analysis based on 70% minimum resemblance levels and is indicated by the dashed line and boxes V-1 and V-2 to the far right of the diagram. Troels-Smith (1955) stratigraphy is shown on the left as well as modelled calibrated ages which were determined using an age-depth model (Clam).
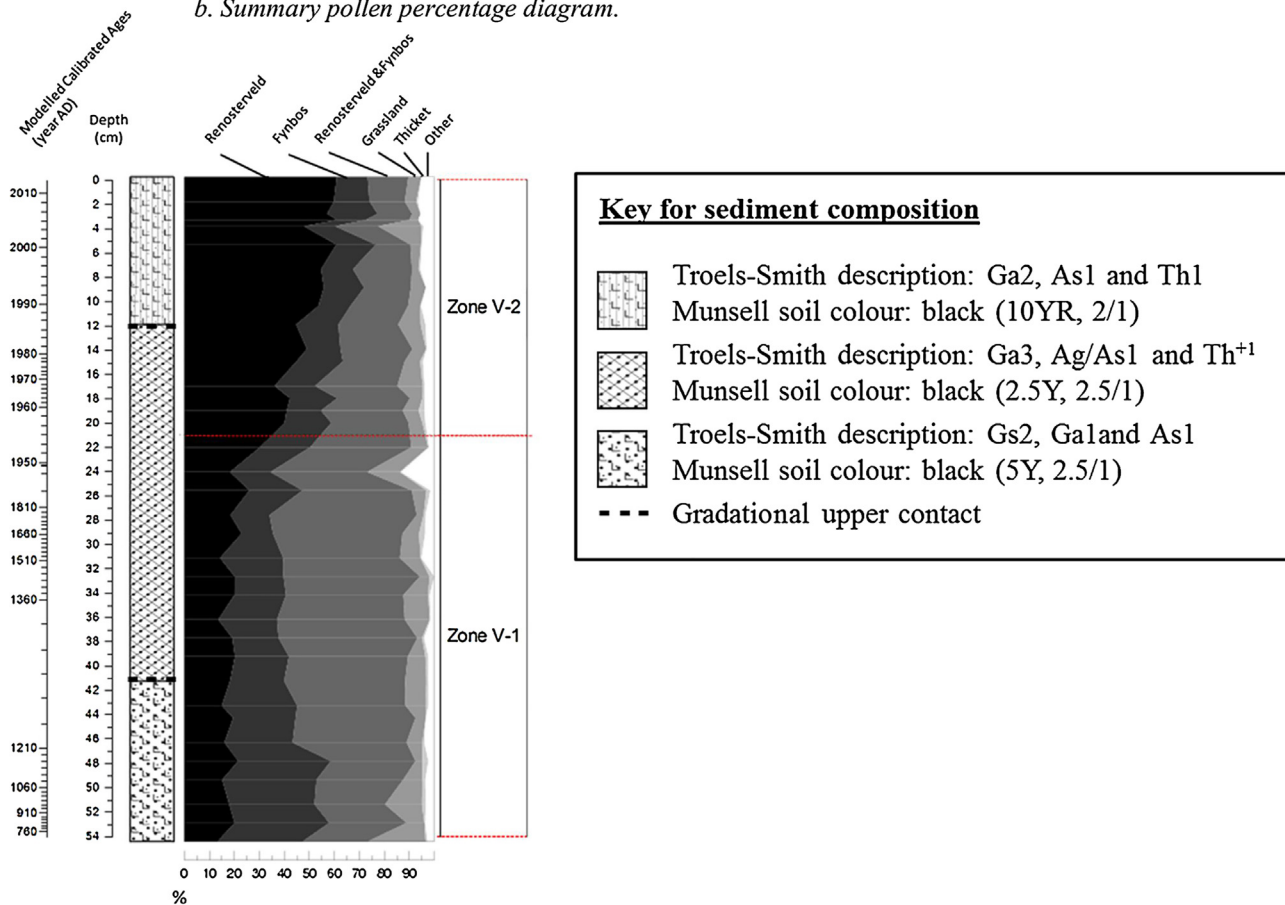
b. Summary pollen percentage diagram.

Fig. 4. (Continued)

The abundance of coprophilous fungal spores were low and mostly absent in this zone. They begin to increase, however, towards the top of Zone V-1. Non-coprophilous spores, such as Trilete and Monolete spores, were also relatively low. Marked differences exist between percentage (Fig. 4a) and concentration data (Fig. S3) for other non-coprophilous spores and this is likely due to the Fagerlind effect. As evident by the percentage data, other non-coprophilous spores comprised a majority of the total spore sum during zone V-1 (mean 78%) and reached a maximum of 97% in ca. CE 1240 (44 cm).

On average, macro-charcoal was lower in Zone V-1 (mean 147.5 particles cm^{-3}) than V-2 and reached its lowest abundance (44 particles cm^{-3}) in Zone V-1. Conversely, micro-charcoal was generally higher (mean 13.6 $cm^2\ cm^{-3}$), more variable and reached its highest abundance of 31.6 $cm^2\ cm^{-3}$ in ca. CE 1350 (37 cm). Other high micro-charcoal peak events occurred in ca. CE 860 (52.5 cm), ca. CE 1150 (48 cm), ca. CE 1260 (42 cm) and ca. CE 1360 (35 cm). Despite the variability in micro-charcoal abundance in the palaeoecological record of the VANG core from ca. CE 750–1400, the pollen data showed very little variation. Some taxa fluctuated slightly (e.g. *Anthospermum*, Poaceae and Restionaceae) whereas most taxa remained stable.

4.4.2. Zone V-2 (16 sub-sample depths; 0–21 cm)

Zone V-2 comprised 16 sub-samples, dating from ca. CE 1955–2012 (21 cm–0 cm). This zone was strikingly different to the underlying zone (V-1) due to the notable increase in Asteraceae *Stoebe/Elytropappus*-type pollen. It reached its highest abundance of 61% in ca. CE 2004 (3.5 cm). Asteraceae long-spine type-1 pollen

was the next most abundant (mean 20%) taxa during Zone V-2 but this trend did not appear in the concentration data (see Supplementary Fig. S3) and was most likely due to the Fagerlind effect. On average, *Cliffortia* (Rosaceae) (mean 0.6%) was slightly more abundant during this zone compared with Zone V-1, whereas the following pollen taxa were all less abundant in Zone V2: *Anthospermum* (Rubiaceae) (mean 4.6%), Ericaceae (mean 2.6%), Proteaceae (mean 1.7%), Restionaceae (mean 5%), Poaceae (mean 6%). Exotic taxa, such as cereal crops (also known as Cerealia), *Eucalyptus* and *Pinus,* occurred in the pollen spectrum for the first time in Zone V-2. Cerealia pollen (mean 0.02%) and *Eucalyptus* (mean 0.02%) are present in low abundances in both the percentage (Fig. 4a) and concentration diagram (Fig. S3) from ca. CE 2000 (5.5 cm) and ca. CE 1976 (15 cm) respectively. *Pinus* is the dominant exotic taxon with an average of 3% in Zone V-2 and its first occurrence was in ca. CE 1957 (20 cm). Total aquatics and marginal pollen types were lower in Zone V-2 (see ratio of aquatics and marginal:terrestrial pollen in Fig. 4a) and declined steadily from 41% in ca. CE 750 (54 cm) to its lowest of 3% in CE 2004 (3.5 cm). The ratio of degraded pollen to undegraded (terrestrial pollen) was slightly lower in Zone V-2 (mean ratio of 0.04) compared to Zone V-1 (Fig. 4a).

Coprophilous fungal spores (*Sporormiella*, Sordariaceae, *Gelasinospora* and *Coniochaeta*) comprised the bulk of the total spore sum in Zone V-2; Sordariaceae (mean 60%) was the dominant spore type in this zone. On average macro-charcoal was higher (mean 537.4 particles cm^{-3}) in Zone V-2 and reached its highest (1100 particles cm^{-3}) in CE 2004 (3.5 cm). On the other hand, micro-charcoal was generally low (mean 9.3 $cm^2\ cm^{-3}$) and less variable.
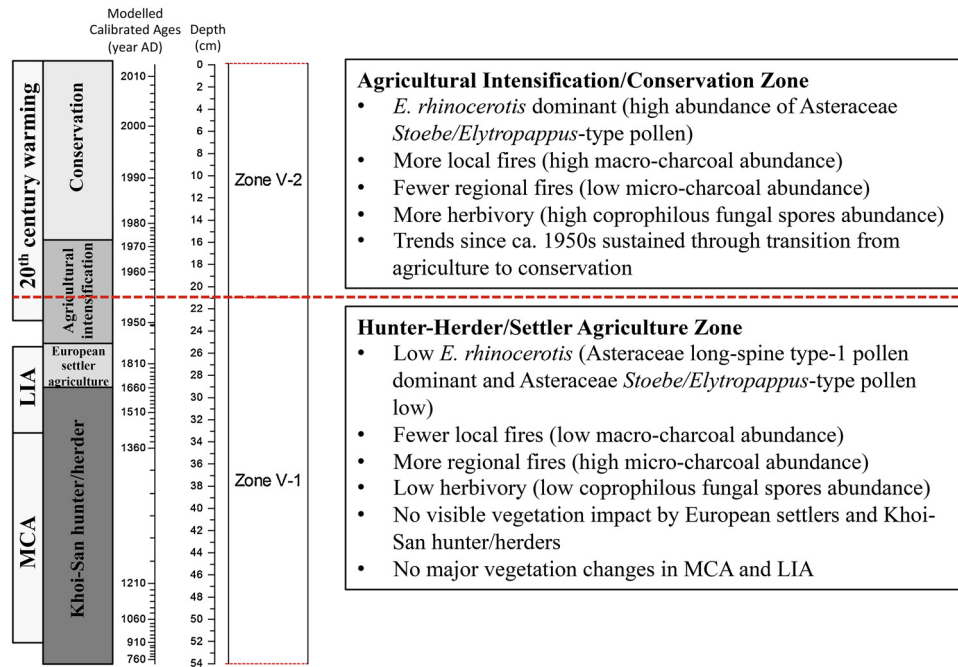
Fig. 5. Schematic summarising how the main findings of the VANG core relate to long-term climate change (i.e. Medieval Climate Anomaly (MCA, ca. CE 900–1400); Little Ice Age (LIA, ca. CE 1400–1800) and 20th century warming) and land-use (i.e. Khoi-San hunter/herders, European settlers, agricultural intensification and conservation period); shown on the far left of the diagram. Pollen zonation is shown: Zone V-1 is the <1950s 'Hunter-Herder/Settler Agriculture Zone' and Zone V-2 is the 1950s-present 'Agricultural Intensification/Conservation Zone'.

5. Discussion

The palaeoecological evidence shows that the Elandsberg PNR vegetation was remarkably stable from the 8th century until the mid-20th century. From the ca. CE 1950s, a significant change occurred with an increase in Asteraceae *Stoebe/Elytropappus*-type pollen (Fig. 4a), which is most likely an increase in Renosterbos (*E. rhinocerotis*). from the ca. CE 1950s, statistical analysis indicates a new pollen zone (Zone V-2), coinciding with an increase in coprophilous fungal spores and macro-charcoal, which suggests increased herbivory and fire, a trend which continues in the ca. CE 1980s (Fig. 4a). In contrast, the pollen data show negligible response to previous climatic anomalies (warm and arid MCA and cool and wet LIA) that are known from regional palaeoclimate reconstructions (Cronin et al., 2003; Haensler et al., 2010; Holmgren et al., 2003; Huang et al., 2000; Lee-Thorp et al., 2001; Mayewski et al., 2004; Stager et al., 2012; Tyson and Lindesay, 1992; Weldeab et al., 2012). Subtle increases in Asteraceae *Stoebe/Elytropappus*-type pollen and coprophilous fungal spores began from the later ca. CE 1800s, probably indicating the influence of European settlement. The results provide evidence that local land-use change, specifically increased grazing pressure and burning, was the main driver of vegetation change at this site from the mid-20th century.

Data from this study show that land-use (disturbance by herbivory and fire) by settler farmers likely drove vegetation change at Elandsberg PNR, since the substantial increase in *E. rhinocerotis* since the ca. CE 1950s was associated with a significant increase in herbivory (coprophilous fungal spores) and local fire (macro-charcoal) (Figs. 4 and 5). This explanation is confirmed by historical records from the study site that indicate that the intensification of agricultural activities including livestock farming, crop cultivation and associated burning characterised the mid-20th century (Becker, 1996; Forbes, 2014). The later transition to conservation management, since proclamation of the reserve in CE 1973 when agriculture was

excluded but large indigenous herbivores were reintroduced, did not cause a reversal of *E. rhinocerotis* dominance, since levels of herbivory and fire were still high relative to pre-1950s levels (Fig. 5; Table S2).

In the western Cape region, agricultural land-use activities intensified from the 20th century onwards (Bergh and Visagie, 1985; Hoffman, 1997). At Elandsberg PNR, these changes only became apparent in the palaeoecological record from the mid-20th century onwards (Fig. 4a). An important conclusion from these results is that prior to the ca. CE 1950s, *E. rhinocerotis* was relatively scarce in the landscape of this site. Although *E. rhinocerotis* is now considered typical of the vegetation type, its dominance in today's Renosterveld fragments is probably more indicative of intensive land-use and associated degradation in recent decades. Another important finding from this study is that historical Renosterveld at the site was not as grassy as has previously been suggested (low Poaceae abundance - Fig. 4) (Cowling et al., 1986; Newton, 2008; Thom, 1954, 1952). These findings support recent studies which report a historical Renosterveld compositional state consisting of a combination of C4 and C3 grasses and shrubs, therefore historically Renosterveld was a grassy-shrubland and not a purely C4 grassland system (Curtis, 2013; Curtis and Bond, 2013; Newton, 2008). These results show a past vegetation state prior to the intensive land-use impacts which occurred at this site in the mid-20th century, which may be a realistic option for a conservation and restoration baseline.

The present study shows only subtle changes in pollen between ca. CE 750–1955 (Zone V-1). Consequently, vegetation at the site was arguably not affected by known past climate changes experienced during this period, such as the warm and arid MCA (ca. CE 900–1400), the cool and wet LIA (ca. CE 1400–1800) and early 20th century warming (Cronin et al., 2003; Haensler et al., 2010; Holmgren et al., 2003; Huang et al., 2000; Lee-Thorp et al., 2001; Mayewski et al., 2004; Stager et al., 2012; Tyson and Lindesay, 1992; Weldeab et al., 2012). Coherent with this finding, other studies showed that, despite palaeoclimatic variability
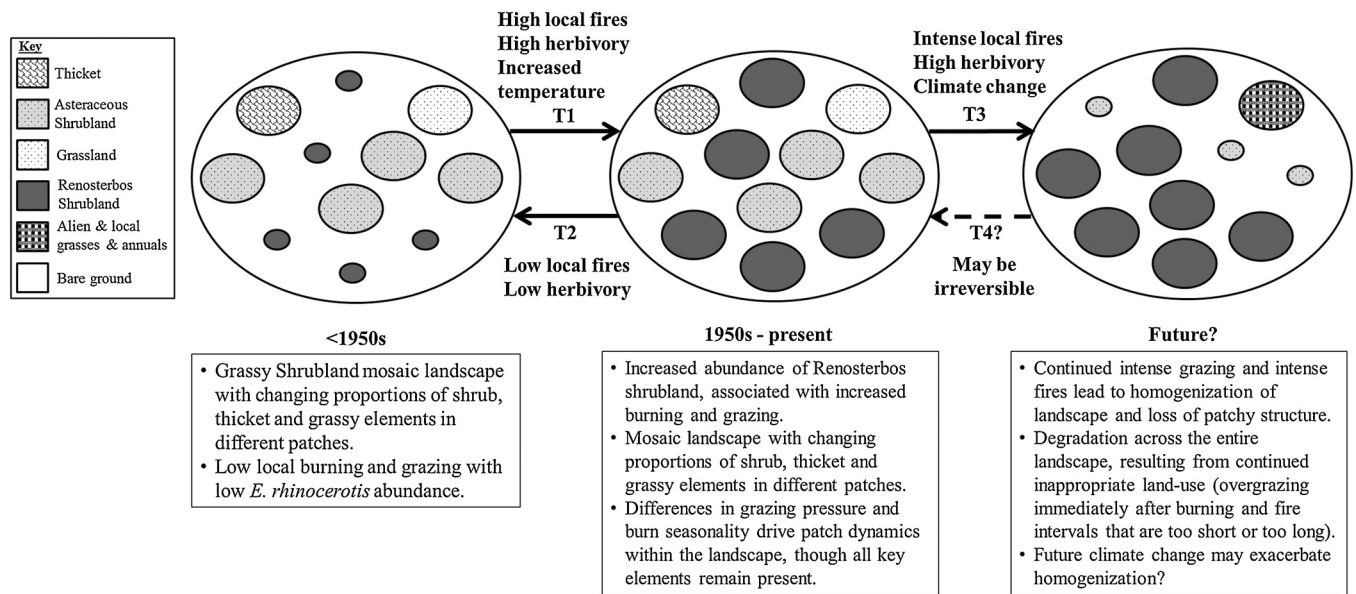
Fig. 6. Conceptual model showing a transition from 'before 1950s' to '1950s-present' (T1) and then to a potential alternative stable state (T3), degraded Renosterveld, once an environmental threshold is crossed in the future. The time taken for a future regime shift is uncertain and the shift could be due to inappropriate levels of land-use disturbance (fire and overgrazing) and/or climate change. Degraded Renosterveld would consist of >60% bare ground, is homogenous at the landscape level and would be dominated by E. rhinocerotis and alien and local grasses and annuals. T1–T4 represent potential transitions and their associated drivers of change.

(evident by stable isotope analyses) in the WRZ, vegetation remained relatively stable (Meadows and Sugden, 1993, 1991; Meadows et al., 2010; Quick et al., 2011). It is possible, however, that turnover within Renosterveld vegetation was not apparent due to low taxonomic resolution of the pollen data.

Although the pollen data showed only subtle changes in composition before the ca. CE 1950 s (e.g. *Anthospermum* spp, Poaceae and Restionaceae), micro-charcoal data suggests high variability in regional fire from ca. CE 750–1400. These findings are partly consistent with those of Meadows and Baxter (1999), who described the pre-colonial period as being abundant in micro-charcoal fragments. No pre-pastoralist baseline exists in the present record for comparing the high micro-charcoal and vegetation stability, so whether the micro-charcoal results are due to land-use by the Khoikhoi pastoralists (Boonzaier, 1996; Hoffman, 1997) or climate variability, specifically the warmer conditions of the MCA, remains uncertain. Relatively low levels of local fire and herbivory occurred during ca. CE 750–1400. This stability persisted throughout occupation by indigenous Khoi-San hunter/herders and throughout the early period of European settlement (see Zone V-1 in Figs. 4 and 5), suggesting that these user groups had little impact on the landscape compared with agricultural intensification from the mid-20th century. European settlement from the CE 1700s is associated with a very slight increase in *E. rhinocerotis* and coprophilous fungal spores, but likewise these changes were apparently not substantial.

The palaeoecological record from ca. CE 1300 to ca. CE 1950s suggests a resilient landscape with little sign of visible climate nor human impact. More palaeoecological records, and of longer duration (>2000 years) are needed to investigate how the arrival and transhumant cycles of Khoikhoi pastoralists might have altered regional fire regimes. We also acknowledge that taxonomic resolution in our pollen data is low, however, and that community composition may have changed (whether due to a response to past climate or land-use) at a species or genus level despite perceived stability at the family level.

Instrumental weather station records provide evidence of increasing temperatures in the WRZ since CE 1901 (Haensler et al.,

2010), but warming likely started earlier than weather station records began, hence probably at the end of the LIA in ca. CE 1800 (Mayewski et al., 2004; Stager et al., 2012). The pollen data do not show a synchronous response with early 20th century warming (Fig. 4a). This response encourages us to think that Renosterveld may be resilient to current climate warming, though with the caveats that thresholds in climate change may be reached in the future and / or that 'no-analog' or novel climate conditions may arise (Altwegg et al., 2014; Williams et al., 2013; Williams and Jackson, 2007). Furthermore, multiple interacting stressors (e.g. climate and land-use) may reduce resilience to climate change. Thus, despite the strong evidence for land-use (herbivory and fire) as the main driver of recent vegetation change, it is possible that anthropogenic climate change characterised by 20th century warming could have been an interacting driver of change in the landscape, which added further stress to the ecosystem.

Landscape structure (patchiness) results from landscape processes which change at a range of spatial and temporal scales. Processes evident at this site include geomorphology (e.g. sedimentation and erosion), herbivory (ecosystem engineers) and fire frequency and intensity. Spatial patchiness can promote community resilience and persistence at landscape scales (Krebs, 1978; Molles, 2008). The apparent resilience of the Elandsberg PNR and its biodiversity value probably links to a heterogeneous, patch-mosaic landscape with a range of different substrates and post-fire ages (Fig. 2a–c). This heterogeneous structure, uneven distribution of biomass and fragmented nature of the landscape provides a range of habitats for plant and animal species. It also reduces the likelihood of large-scale fires. Results from this study suggest that fire and grazing regimes over the last ca. 60 years have been inappropriate, with anomalously high levels of disturbance by fire and herbivory associated with an increasing abundance of *E. rhinocerotis* compared with pre-colonial times. Increased herbivory would have exposed soil and therefore increased runoff and sedimentation rate (Foster et al., 2007; Gell, 2010; Rietkerk et al., 2000), as is evident from the ca. CE 1950 s (Zone V-2; Fig. 4a). Patches of vegetation with high *E. rhinocerotis* abundance have been observed in Elandsberg PNR. Low biodiversity characterises

these patches, with 60% bare ground consisting mainly of stones and the remaining 40% being vegetation comprising predominantly *E. rhinocerotis* (see 'Shale Renosterveld' vegetation unit in Fig. S2).

Despite the unprecedented increase in local fires, herbivory and *E. rhinocerotis* abundance since ca. CE 1950s, however, key elements of the system are still present, including fire sensitive thicket taxa (i.e. *Searsia*, *Ilex* and Oleaceae) (Fig. 4a). The continued presence of thicket taxa in the pollen record, alongside increasing *E. rhinocerotis,* suggests that, despite the increase in disturbance (altered fire regime and increased herbivory) over time, the landscape is still heterogeneous with thicket patches that act as fire refugia, and thereby contribute to the maintenance of biodiversity. The presence of these key elements could mean that the current degraded state is probably reversible if immediate action is taken by the reserve managers, specifically a reduction in the abundance of reintroduced indigenous herbivores, and a reduction in fire frequency (Fig. 6; e.g. T2).

Results of this study suggest that the Elandsberg PNR ecosystem underwent a transition from low to high levels of *E. rhinocerotis* when local herbivory and fire were increased during the mid-20th century. The conceptual model proposed incorporates low and high *E. rhinocerotis* states (Fig. 6, T2 and T1, respectively) (Cowling et al., 1986; Milton, 2007; Rebelo, 1995) as well as a hypothetical third landscape state that may occur if intensive burning and grazing continues in the future (Fig. 6, T3). In this third state, we suggest that heterogeneity and patchiness would be lost, and as a result, fire refuges and other specialised habitats would disappear from the landscape, leading to an overall reduction in biodiversity. Such a change might be precipitated if changes in rainfall, temperature, wind and relative humidity and CO_2 (Hoffman et al., 2011), as well as increased fire ignitions due to human population growth, all act in concert to increase fire intensity and frequency. If landscape homogenisation occurs, it may be difficult to reverse (Fig 6, T4), as fire sensitive elements could be lost from the landscape, and the diversity of post-fire ages could be reduced (Folke et al., 2004). A more homogenous vegetation structure could lead to more widespread fires, reinforcing the loss of patchiness. In order to prevent an irreversible regime shift in the future, we recommend that environmental managers at Elandsberg PNR need to alter the land-use activities specifically by reducing grazing and burning.

The results of this study suggest that maintaining patchiness and preventing homogenisation of vegetation requires low and variable levels of fire and herbivory. Such a disturbance regime would simulate that of a pre-1950s or pre-colonial period and could provide the sort of conditions favourable for a reduction in *E. rhinocerotis* and increase in patchiness and heterogeneity in the landscape. The nature of the palaeoecological record does not allow us to recommend specific grazing and burning regimes. Therefore, experimental manipulation of fire seasonality, intensity and frequency is required. The aim of the fire management experiment would be to identify how best to maintain heterogeneity through patch burns that retain a range of post-fire ages to ensure biodiversity conservation, future resilience and the maintenance of ecosystem services. Similarly, changes in herbivore density and grazing enclosures/exclosures will be needed to help identify appropriate levels of grazing. Vegetation monitoring is also needed so that any effects of climate change can be identified and responded to.

6. Conclusions

Inaccurate perceptions of past conditions based on relatively short-term perspectives often provide misleading reference points for environmental management and restoration. This study illustrates that even decadal-scale data may provide inappropriate management goals. Future conservation planning, management goals and possibly restoration targets requires a long-term, palaeoecological-perspective. The present study has revealed a pre-1950s baseline or even better, a pre-colonial baseline, as an appropriate management target for Elandsberg PNR, because grazing, fire frequency and the dominance of *E. rhinocerotis* has been anomalously high from the mid-20th century, compared with the rest of the past ca. 1300 years. Experimental research and adaptive management are needed to determine the effects and interactions between different fire seasonality and grazing regimes. These approaches should continue in the future as climate changes. Further palaeoecological research throughout the Renosterveld region will enhance our understanding and management of this critically endangered but poorly understood vegetation type.

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